



Research

Cite this article: Simpson RK, Johnson MA, Murphy TG. 2015 Migration and the evolution of sexual dichromatism: evolutionary loss of female coloration with migration among wood-warblers. *Proc. R. Soc. B* **282**: 20150375. <http://dx.doi.org/10.1098/rspb.2015.0375>

Received: 17 February 2015

Accepted: 29 April 2015

Subject Areas:

evolution, behaviour, ecology

Keywords:

evolutionary loss, female ornamentation, sexual dimorphism, latitudinal gradient, social selection, sexual selection

Author for correspondence:

Troy G. Murphy

e-mail: troy.murphy@trinity.edu

[†]Present address: School of Life Sciences, Arizona State University, Tempe, AZ 85281, USA.

Migration and the evolution of sexual dichromatism: evolutionary loss of female coloration with migration among wood-warblers

Richard K. Simpson[†], Michele A. Johnson and Troy G. Murphy

Department of Biology, Trinity University, San Antonio, TX 78212, USA

RKS, 0000-0002-1319-8197; TGM, 0000-0001-7239-2160

The mechanisms underlying evolutionary changes in sexual dimorphism have long been of interest to biologists. A striking gradient in sexual dichromatism exists among songbirds in North America, including the wood-warblers (Parulidae): males are generally more colourful than females at northern latitudes, while the sexes are similarly ornamented at lower latitudes. We use phylogenetically controlled comparative analysis to test three non-mutually exclusive hypotheses for the evolution of sexual dichromatism among wood-warblers. The first two hypotheses focus on the loss of female coloration with the evolution of migration, either owing to the costs imposed by visual predators during migration, or owing to the relaxation of selection for female social signalling at higher latitudes. The third hypothesis focuses on whether sexual dichromatism evolved owing to changes in male ornamentation as the strength of sexual selection increases with breeding latitude. To test these hypotheses, we compared sexual dichromatism to three variables: the presence of migration, migration distance, and breeding latitude. We found that the presence of migration and migration distance were both positively correlated with sexual dichromatism, but models including breeding latitude alone were not strongly supported. Ancestral state reconstruction supports the hypothesis that the ancestral wood-warblers were monochromatic, with both colourful males and females. Combined, these results are consistent with the hypotheses that the evolution of migration is associated with the relaxation of selection for social signalling among females and that there are increased predatory costs along longer migratory routes for colourful females. These results suggest that loss of female ornamentation can be a driver of sexual dichromatism and that social or natural selection may be a stronger contributor to variation in dichromatism than sexual selection.

1. Introduction

The evolution of sexually dimorphic ornamentation has long been of interest to biologists [1]. Historic explanations have centred on the hypothesis that male and female ornamental phenotypes are driven apart when males are subject to positive directional selection for sexual signalling, while females maintain a non-signalling phenotype [2]. This hypothesis proposes that selection, acting on males, drives male ornamental expression away from a naturally selected optimum for crypsis [3]. However, this viewpoint does not acknowledge that sexual differences in ornamentation can arise owing to evolutionary changes in female signalling phenotype (for review, see [2,4]). In recent decades, the study of sexual/social signalling has shifted towards considering evolutionary changes in females [5–8]. Research has provided compelling evidence that the female ornamental phenotype is not under strong constraint due to genetic correlation and that female ornamental traits can change independently of male phenotype [9,10]. Such changes in female ornamentation have been inferred from recent research demonstrating female-specific functions of

ornamentation in communication [11,12] and from comparative studies which have shown that female ornamental phenotype is evolutionarily labile, either becoming more or less exaggerated when compared with male ornamentation [5,10,13–16]. A notable example comes from Martin and Badyaev's work, indicating that females evolve drabber plumage when they are subject to greater nest predation [6]. These studies indicate that the evolutionary loss of character states, in either males or females, may be an important driver of sexual dichromatism [15,17], and underscore the need to focus on selective pressures acting on female phenotypes to better understand signal evolution [18].

Among North American birds, there is a remarkable geographical pattern in sexual dimorphism, wherein sexual dichromatism becomes more pronounced at higher latitudes: females tend to be less ornamented than males among species breeding at northern latitudes, while species breeding at southern latitudes tend to have similarly colourful males and females [19,20]. This latitudinal gradient has been noted broadly across North American passerines [19] and waterfowl [21], and specifically across New World orioles and wood-warblers [22]; however, only the waterfowl study was analysed in a phylogenetic context. Although this geographical gradient has been widely recorded, little comparative research has tested how changes in female phenotype contribute to this pattern (but see [5,8,14]).

Here, we use phylogenetically controlled comparative analyses to test three non-mutually exclusive hypotheses for the evolution of sexual dichromatism among New World wood-warblers, a group in which sexual dichromatism increases along a latitudinal gradient [22]. The first two hypotheses are female-centric and posit that dichromatism arose due to female loss of coloration with the evolution of migration. The first proposed mechanism is that females face greater net costs, compared with males, of being colourful during migration owing to risks of being detected by visual predators. Because males are expected to gain greater reproductive benefits from ornamentation on breeding grounds, we expect predation costs to have a more substantial net-negative effect on female ornamentation, and for these costs to drive female colour away from the male-like phenotype. There is compelling evidence that predation by visual predators is high along migratory routes [23,24], that coloration can increase susceptibility to predation [25–27] and that mortality increases with migratory distance [28]. We thus propose that the cost of being colourful increases with migratory distance owing to greater exposure to visual predators. This 'migration cost hypothesis' has not previously been tested, and predicts that the evolution of migration will occur in concordance with the evolution of dichromatism and that the degree of sexual dichromatism will increase with migration distance.

The second proposed mechanism regarding female loss of coloration posits that once migration evolves, females are released from positive selection pressure for signalling. This hypothesis has been proposed previously [8] and derives from the observation that migratory species typically do not invest in territorial defence [29], while females of many non-migratory species do [30,31]. Furthermore, there is growing evidence that female ornamentation is favoured for territorial and resource defence [5,30,32–36], especially among non-migratory birds where territories are maintained year-round [36–38]. As such, this 'relaxed social selection

hypothesis' proposes that female ornamentation is selectively disfavoured among migratory species, not because of the costs of migration (as per the first hypothesis), but because migratory females are no longer gaining the selective benefits associated with signalling during territorial defence. Similar to the 'migration cost hypothesis', this hypothesis predicts that the evolution of migration will occur in concordance with the evolution of sexual dichromatism, but this hypothesis makes no prediction about migratory distance.

In addition, we test a third, male-centric hypothesis that focuses on increases in male ornamentation with breeding latitude. This hypothesis proposes that sexual dichromatism will increase with breeding latitude because sexual selection is stronger at northern latitudes [20]. There is evidence that the shortened breeding season at northern latitudes favours male–male competition [39,40], leading to greater opportunity for selection because synchronized breeding reduces costs to females exhibiting mate choice [41] and because breeding synchrony leads to an increased opportunity for extra-pair copulations [42,43]. Thus, this 'breeding-latitude hypothesis' proposes that there will be greater sexual selection for male ornamentation with increasing latitude, and thus predicts that sexual dichromatism will increase with breeding latitude.

The family Parulidae is a diverse group that varies greatly in sexual dichromatism, seasonal migration distances and breeding latitude [44,45]. To test the three hypotheses for the evolution of sexual dichromatism among wood-warblers, we used phylogenetically controlled comparative methods to correlate sexual dichromatism with the following three variables: (i) migratory presence or absence, which tests both the 'migration cost hypothesis' and the 'relaxed social selection hypothesis'; (ii) migratory distance, which tests the 'migration cost hypothesis'; and (iii) breeding latitude, which tests the 'breeding-latitude hypothesis'. We additionally determined the ancestral character state of both sexual dichromatism and migratory behaviour among the entire clade of wood-warblers to assess the origin of elaborate female characters within this group and to assess ancestral patterns of migration. Results from these tests will indicate whether a significant amount of variation in sexual dichromatism can be attributed to the loss of female coloration or to the gain of male coloration.

2. Material and methods

(a) Natural history of study group

There are 108 species of wood-warblers (this includes two genetically distinct subspecies, see figure 1), and although they range widely through the New World and are distributed both above and below the equator, all of the migratory species ($n = 48$) migrate north for the breeding season and south for the winter [44]. Some wood-warblers have two distinct plumages per year; however, the pre-alternate moult (moulting into breeding plumage) occurs while on the wintering grounds, so all migratory wood-warblers fly northwards in their breeding plumage.

(b) Quantifying sexual dichromatism

To quantify sexual dichromatism in colour and pattern, we calculated a sexual dichromatism score for each species of wood-warblers based on plumage colour and pattern differences between males and females. Following Martin *et al.* [47], we used a human visual ranking system to calculate this score.

degree of dichromatism. Observers were presented with images of a male and female from one dichromatic species at a time, and all notations of male and female designation on the images were removed. To encourage detailed observation of plumage differences between the sexes, observers were asked to write down three visible differences for each male–female pair. When the HBW recognized subspecies, we used sequential coin tosses to randomly select one representative subspecies. Scores given by different observers were highly similar (intra-class correlation = 0.74, $F_{47,188} = 15.53$, $p < 0.001$). Using scores from the five observers, we computed a mean dichromatism score for each dichromatic species.

(c) Quantifying migration distance and breeding latitude

Migration distance was determined for each species using GIS mapping software, DIVA-GIS v. 7.5 [52], and species range maps were downloaded from www.natureserve.org [53]. We measured migration distance by a centroid distance for each species, defined as the distance between the latitude of the centroid within the wintering range to the latitude of the centroid of the breeding range. We determined centroids (or geometric centre) by tracing the perimeter of each seasonal range and used DIVA-GIS to calculate the arithmetic mean of the resulting polygons. To measure the latitudinal distances between the breeding and wintering centroids, we used Geographic Distance Matrix Generator from the American Museum of Natural History [54]. For three species (*Setophaga pitiayumi*, *Basileuterus lachrymosa* and *Cardellina rubrifrons*), it was not clear whether the species was migratory (i.e. only subpopulations migrated, or altitudinal migrations occurred), and we identified them as non-migratory following the designations of Winger *et al.* [45]. All statistical analyses (see below) were run both with these three species included and with them excluded. Results from these two approaches were qualitatively similar, so we report here only the analysis that included these species.

Breeding latitude was determined by the centroid latitude of the breeding range. For non-migratory species, we used the centroid of the year-round range as the breeding latitude. For species that breed south of the equator (non-migrants only; $n = 21$), we positivized breeding latitudes, allowing our measure to represent distance from the equator and degree of seasonality.

(d) Relationship between sexual dichromatism: migration, migration distance and breeding latitude

We addressed the following questions: does dichromatism in wood-warblers relate to: (i) the presence or absence of migration, (ii) migratory distance, and (iii) breeding latitude. All statistical analyses were conducted in the statistical computing environment R [55]. For all analyses, we used the robust wood-warbler phylogeny from Lovette *et al.* [46], recently resolved using two mitochondrial DNA regions and six nuclear DNA loci, and estimated using RAXML maximum-likelihood analysis (figure 1). The phylogeny included one recent polytomy involving *Geothlypis flavovellata*, *Geothlypis trichas* and *Geothlypis nelsoni*. We dealt with this polytomy by conducting our analyses of the entire Parulidae clade using three trees, each including one of the three possible resolutions of the polytomy; however, because results from these analyses were qualitatively the same, we present the results based on one arbitrarily chosen tree (with *G. flavovellata* and *G. trichas* as sister taxa). In all analyses, we used Pagel's λ as a measure of phylogenetic signal and calculated λ from the residuals of each model [56].

To test whether dichromatism is related to the presence or absence of migration, we used phylogenetic ANOVA [57]

conducted with the *phytools* packages in R [58]. To test whether dichromatism was related to migration distance and/or breeding latitude, we used a combination of phylogenetic least-squares analyses (PGLS [56]) and Akiake's information criteria (AIC), which enabled us to test the relative explanatory power of migration distance and breeding latitude on the evolution of sexual dichromatism, while allowing for the possibility that all hypotheses could be supported (i.e. both natural selection for dull female ornamentation and sexual selection for exaggerated male ornamentation may occur simultaneously). The AIC approach is appropriate here because the two variables are highly correlated (PGLS: $p < 0.0001$, $R^2 = 0.66$), and AIC analysis is robust to collinearity [59,60]. We conducted PGLS analysis through the R package *nlme* [61] to compare univariate models of migratory distance and breeding latitude, a combination model that included both distance and latitude, and a null model, and we calculated Δ AIC, Akaike weights, and the evidence ratio of each model.

To further explore whether there is an increase in dichromatism with migratory distance, we analysed only migratory wood-warblers, using the same combination of PGLS [56] and AIC described above. For this analysis, we pruned the wood-warbler phylogeny of all non-migratory species using the *drop.tip* command in the R package *ape* [62].

(e) Correlated evolution between migration and dichromatism

To test for an association between evolutionary transitions in the presence or absence of migratory behaviour with the presence or absence of sexual dichromatism, we use the concentrated changes test (CCT [63]), which tests for associations between the gains and losses of each trait. We used MACCLADE v. 4.0 [64] to perform the CCT using migratory behaviour as our independent character. We used both character optimization techniques (DELTRAN and ACCTRAN [64]) to remove ambiguity in the evolutionary reconstructions of each character and performed CCT on each reconstruction. Results from both reconstructions were qualitatively the same, so we only present results from the ACCTRAN optimization. In addition to using the CCT, we used Pagel's correlated test [65] to evaluate models of independent and dependent evolution between migratory behaviour and the presence or absence of dichromatism. This analysis was conducted using MESQUITE [66].

(f) Ancestral state reconstruction of dichromatism and migration distance

To estimate sexual dichromatism of the most recent common ancestor of all wood-warblers, we sorted sexual dichromatism scores into four categories: (i) monochromatic; (ii) low sexual dichromatism (dichromatism scores between = 1.0–1.9; mean \pm s.e. = 1.4 ± 0.08 , $n = 14$); (iii) medium sexual dichromatism (scores between = 2.0–2.9; 2.3 ± 0.08 , $n = 18$); and (iv) high sexual dichromatism (scores between = 3.0–4.0; 3.5 ± 0.09 , $n = 14$).

We used the *ace* command in the R package *ape* [62] to conduct ancestral state reconstruction of sexual dichromatism and migration distance. For our ancestral state reconstruction of the discrete measure of sexual dichromatism, we used an approach following methods of Schluter *et al.* [67], which calculates state likelihoods at each node to determine the final maximum likelihood of the ancestral state. In our analysis, we assumed that transitions between dichromatism occurred with equal rates. We also conducted an ancestral state reconstruction of the presence or absence of migration, as was previously reported in Winger *et al.* [45], following methods described above.

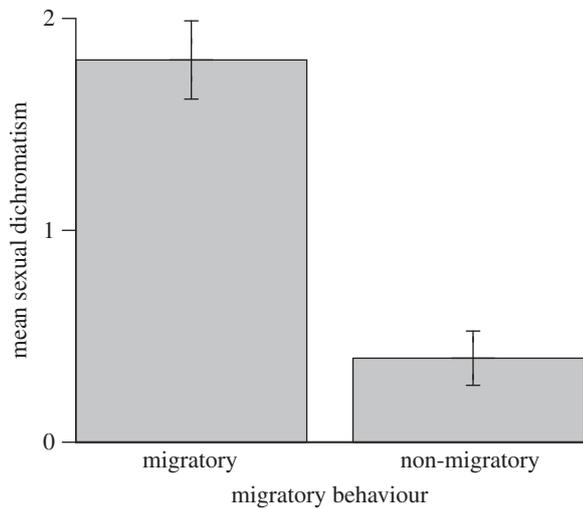


Figure 2. Mean sexual dichromatism score (error bars: \pm s.e.) between non-migrants and migrants for all of wood-warblers.

3. Results

(a) Sexual dichromatism versus presence/absence of migration

Our analysis of the binomial categorization of the presence or absence of migration indicated that migratory wood-warblers exhibited greater sexual dichromatism (mean \pm s.e. dichromatism score = 1.8 ± 0.18 , $n = 48$) than did non-migratory species (0.4 ± 0.13 , $n = 60$; ANOVA: $F_{1,106} = 41.5$, $p = 0.002$; figure 2). Monochromatism was very common among non-migrating species (51 out of 60, 85%), and far less prevalent among migratory wood-warblers (11 out of 48, 23%; $\chi^2_1 = 39.5$, $p < 0.0001$). These results indicate that migratory species are more likely to be dichromatic, and have a higher degree of dichromatism, than non-migratory species.

(b) Sexual dichromatism versus migration distance and breeding latitude

When comparing four models predicting sexual dichromatism (migration distance, breeding latitude, combination of both migration distance and breeding latitude, and null), the strongest model was the migration distance model (Akaike weight = 0.60; table 1). The migration distance model significantly predicted sexual dichromatism ($p < 0.0001$; $R^2 = 0.26$), with a significant phylogenetic signal ($\lambda = 0.74$, $p < 0.0001$). Additionally, the migration distance model was almost twice as likely as the next highest model—the combination model (Akaike weight = 0.38, Δ AIC = 0.93, evidence ratio = 1.6). Further, the migration distance model was many times more likely than either of the remaining models—the breeding latitude model (Akaike weight = 0.02, Δ AIC = 6.62, evidence ratio = 27.3) and the null model (Akaike weight < 0.01, Δ AIC = 30.50, evidence ratio > 100).

When an identical analysis was conducted on the pruned dataset including only migratory wood-warblers, the strongest model was again the migration distance model (Akaike weight = 0.44; table 2). The migration distance model significantly predicted sexual dichromatism ($p = 0.049$; $R^2 = 0.08$) and there was a significant phylogenetic signal in this trait ($\lambda = 0.74$, $p = 0.04$). The migration distance model was over twice as likely as any of the other models—the breeding-

Table 1. Results from AIC analyses on all wood-warblers, evaluating four possible models for the evolution of sexual dichromatism. (All models were conducted using PGLS.)

model	AIC	Δ AIC	Akaike weight	evidence ratio
migration distance	282.5	—	0.60	—
migration distance + breeding latitude	283.5	0.93	0.38	1.6
breeding latitude	289.2	6.62	0.02	27.3
null	313.0	30.50	0.00	> 100

Table 2. Results from AIC analyses on only migratory wood-warblers, evaluating four possible models for the evolution of sexual dichromatism. (All models were conducted using PGLS.)

model	AIC	Δ AIC	Akaike weight	evidence ratio
migration distance	151.3	—	0.44	—
migration distance + breeding latitude	152.8	1.44	0.21	2.1
breeding latitude	153.0	1.69	0.19	2.3
null	153.3	1.95	0.16	2.7

latitude model (Akaike weight = 0.21, Δ AIC = 1.44, evidence ratio = 2.1), the combination model (Akaike weight = 0.19, Δ AIC = 1.69, evidence ratio = 2.3) and the null model (Akaike weight = 0.16, Δ AIC = 1.95, evidence ratio = 2.7). Similar to the above analysis on the entire clade of wood-warblers, these results indicate that migration distance has more explanatory power than breeding latitude and indicate that an incremental increase in migratory distance is associated with a concomitant increase in dichromatism.

(c) Correlated evolution between migration and dichromatism

When evaluating the concordant evolution of migratory behaviour and sexual dichromatism, we found 14 changes in the presence or absence of sexual dichromatism (eight gains and six losses), and these changes were significantly associated with evolutionary changes in migratory behaviour (Pagel's correlation test: $p < 0.0001$). In particular, three gains of sexual dichromatism were coupled with gains in migration at the same node, and three losses of sexual dichromatism were coupled with losses of migration at the same node, while most other gains/losses followed similar patterns through relative associations. In addition, we found that the dependent evolutionary model was significantly more likely (log likelihood = -77.2) than the independent evolutionary model (log likelihood = -94.7) for the evolution of sexual dichromatism and migratory behaviour (likelihood ratio test = 17.5, $p < 0.0001$). Thus, the evolution

of sexual dichromatism is significantly related to the evolution of migratory behaviour.

(d) Ancestral state reconstruction of sexual dichromatism and migration distance

Using categorical measures of monochromatism and dichromatism, our ancestral state reconstruction for sexual dichromatism demonstrated overwhelming support for the hypothesis that 'monochromatism' was the most likely character state for the ancestor of wood-warblers (likelihood = 0.92; figure 1). Our reconstruction of migratory behaviour mirrored Winger *et al.* [45] and supported the hypothesis that the ancestral wood-warbler was a migrant (likelihood = 0.91; figure 1).

4. Discussion

To examine evolutionary pressures that underlie the often-noted latitudinal gradient of sexual dichromatism found among many North American avian taxa [19,22], we studied evolutionary transitions in dichromatism among wood-warblers. We tested two hypotheses that focused on mechanisms for the loss of female ornamentation with migration, and one hypothesis that focused on the gain of male elaboration with increasing breeding latitude. We found that migration itself was strongly associated with increased sexual dichromatism and that this pattern was largely driven by the gain of dichromatism. Second, we studied graded transitions in dichromatism and found that the distance a species travels during migration was positively related to sexual dichromatism, wherein long-distance migrants tended to be represented by species with distinct males and females, while the sexes of short-distance migrants were more similar to one another. At the same time, our models failed to indicate that breeding latitude was strongly associated with increased sexual dichromatism, when compared with migration distance, thus demonstrating that changes in male coloration were not a strong driving force for the evolution of sexual dichromatism. Furthermore, our ancestral state reconstruction provided strong support for the hypothesis that the ancestor of wood-warblers was monochromatic, indicating that sexual differences in plumage elaboration represents a derived trait within this clade. Taken together, these results suggest that the sexual differences in ornamentation of many migratory wood-warblers arose, at least in part, due to the loss of female coloration. These results highlight the importance of considering evolutionary changes to female signal phenotype, and how the loss of female ornamentation can drive the evolution of sexual dichromatism.

Based on these results, we suggest that two mechanisms (relaxed social selection, and costs associated with migrating long distances) have simultaneously accounted for the loss of elaborate female plumage among many migratory wood-warblers. We propose a two-tiered effect of migration on female ornamentation, where the advent of migration leads to a relaxation of selection for signalling on females, and that once released from signalling, the cost of maintaining colourful plumage while migrating long distances further leads to a reduction in female ornamentation.

The first mechanism underlying the reduction in female ornamentation with migration involves the loss of signalling

benefits to females, wherein migratory females no longer benefit by maintaining elaborate plumage that was previously used to communicate fighting ability during territorial defence (i.e. signal of status [68]). This hypothesis is consistent with previous work indicating that most migratory females arrive on breeding grounds after the males, and that migratory females play little role in territorial defence [29] and, as such, have reduced benefits associated with signals of status. By contrast, female territorial defence commonly occurs in non-migratory tropical species [30,31], and a growing body of literature supports the functional role of female ornamentation in mediating social conflict [35], especially among year-round residents [38,69]. We propose that after migration evolved in some groups of wood-warblers (e.g. *Setophaga*), females faced reduced selection for status signalling, and then drift or selection for crypsis reduced female ornamental phenotype away from the ancestral male-typical expression. This interpretation is in agreement with previous work indicating a link between the evolution of sexual dichromatism and the presence of migration ([6], but see [14]; see [17] for a similar pattern in sexual dimorphism in song). If this interpretation is correct, then the often-noted geographical pattern of sexual dichromatism seen in many avian taxa may have arisen, in part, because selection pressures for signalling have been relaxed in females of migratory species. It is also interesting to consider that there are fewer year-round residents as one moves north from the tropics [29]. As such, the observation that breeding latitude contributes to some of the variation in sexual dichromatism may not reflect increasing sexual selection in males with breeding latitude (i.e. the breeding-latitude hypothesis), as has been proposed, but instead may indicate that females which breed further from the equator are released from signalling for territorial defence. To address this hypothesis, we recommend that future research test for a reduction along a latitudinal gradient of both female territoriality and the use of female ornamentation to signal status.

The second proposed mechanism to account for the loss of ornamentation among migratory females is that coloration is costly to maintain during migration. Migration is known to negatively affect fitness in a number of ways, especially owing to predation when migrants find themselves in reduced energetic condition at stopover sites in unfamiliar locations or habitats [23,24,70]. There is evidence that coloration can increase susceptibility to predation [25–27] and that predation risks increase with greater dispersal distance [71]. In addition, recent evidence indicates that long-distance migrants suffer greater mortality than short-distance migrants [28], which may occur, in part, due to increased predation risks with migratory distance. In addition to predation, the costs of producing coloration may further add to the costs faced by colourful migrants [72]. Producing colourful traits, such as carotenoid-based plumage, may be costly because once these dietary derived compounds are deposited in feathers, they are unavailable for other physiological functions [73,74]. As such, a trade-off may exist between the degree of ornamentation and physiological performance during a migration. Irrespective of the specific costs associated with being colourful while migrating, our results, which demonstrate a positive relationship between migratory distance and dichromatism, are consistent with the hypothesis that costs increase in concert with migration distance. Although our results indicate that this pattern is heavily driven by

the evolution migration behaviour (see discussion above on the relaxed social selection hypothesis), the positive relationship between dichromatism and migratory distance persists, though to a lesser degree, when analysing only migratory wood-warblers. This study provides, to our knowledge, the first support for the 'migration distance hypothesis' and provides compelling evidence that costs associated with ornamentation can lead to evolutionary losses in character states that lead to sexual dichromatism.

Although increasing breeding latitude is likely to result in an increase in the opportunity for sexual selection acting on males [20], our models indicate that breeding latitude was not as strongly supported as migratory distance in predicting sexual dichromatism. As such, it appears that evolutionary increases in male ornamentation are not the primary driving force behind the evolution of sexual dichromatism (as has been generally assumed), but rather, that changes in female ornamentation are more likely to contribute to the evolution of sexual dichromatism. These results provide cautionary evidence that researchers should be hesitant to use sexual dichromatism as an indicator of the strength of sexual selection acting on males (as is often done in comparative research) because, even when comparing highly dimorphic species to monomorphic species, the differences in the sexes may arise owing to changes in female characters.

Our current study found that the ancestor of Parulidae was a ~~non~~-migrant, which is in agreement with previous work on this clade [45]. ^{However,} these results indicated that many derived ~~non~~-migratory clades descended from non-migratory ancestors (*Setophaga*, *Cardellina* and *Geothlypis*; figure 1), and our correlated evolution test indicated that when migration was gained there was a significant pattern of concordant changes from monochromatism to dichromatism, further supporting for the hypotheses that females lost coloration with migration. In addition, we found that losses in migratory behaviour were concordant with losses of dichromatism. We note that the associated pattern between migration and dichromatism is not as strong within clades that maintained migration from a migratory ancestor (see *Oreothlypis*, figure 1), while this pattern is prevalent among groups that lost migratory behaviour, or those that lost and then subsequently regained migratory behaviour (see *Setophaga*, figure 1). Taken together, these results provide strong support for the hypothesis that the loss of female coloration is linked to evolutionary transitions in migratory behaviour.

In conclusion, this study tested multiple hypotheses for the evolution of sexual dichromatism among wood-warblers, and our results shed light on the often-noted geographical pattern of increased sexual dichromatism with latitude. We provide strong support for the hypothesis that the ancestral character state for females was monochromatic and that dichromatism among wood-warblers often arose owing to the loss of female coloration. In testing for the mechanisms underlying these changes, we found support for two female-centric hypotheses that focus on evolutionary loss of female coloration, rather than increases in male coloration. Although it has long been understood that selection on male ornamentation influences the evolution of sexual dichromatism owing to varying strengths of social or sexual selection, research in recent decades has correctly emphasized that much remains to be learned about how selection operates on elaborate traits in females [9,18,38,75]. Our current study provides evidence that social and natural selection can be a driver of sexual dichromatism and may be a stronger contributor to variation in dichromatism than sexual selection. Like other recent studies focusing on the evolution of sexual dichromatism, we urge future research on sexual patterns in ornamentation to consider that losses in female ornamentation may strongly contribute to the evolution of sexual dichromatism.

Data accessibility. All data used in analyses are publicly available at the Trinity University Digital Commons (http://digitalcommons.trinity.edu/bio_faculty/56/).

Authors' contributions. T.G.M. conceived of the study; R.K.S. and T.G.M. designed the study and collected the data; R.K.S., M.A.J. and T.G.M. analysed the data; R.K.S. and T.G.M. drafted the manuscript; and all authors edited and approved the final version for publication.

Competing interests. We declare we have no competing interests.

Funding. T.G.M. was supported by the Faculty Development Fund and R.K.S. was supported by undergraduate research funding through the Biology department at Trinity University.

Acknowledgements. We thank Irby Lovette and co-authors for sharing their wood-warbler phylogeny. We are grateful to Trinity University students for scoring dichromatism. We also thank David Ribble, Jeremy Donald and Paulo Pulgarin-Restrepo for help with GIS methods; Keith Tarvin and Russell Ligon for help with statistical analyses, and Liam Revell for advice on phylogenetic analysis. Keith Tarvin, Bruce Lyon, David Ribble and two anonymous reviewers provided useful comments on a previous version of the manuscript. We thank Trinity University Department of Biology for providing the resources to complete this study.

References

1. Darwin C. 1871 *The descent of man, and selection in relation to sex*. London, UK: John Murray.
2. Wallace AR. 1889 *Darwinism*. London, UK: MacMillan and Co.
3. Fisher RA. 1930 *The genetical theory of natural selection*. Oxford, UK: Clarendon.
4. Omland KE, Hofmann CM. 2006 Adding color to the past: ancestral state reconstruction of bird coloration. In *Bird coloration volume 2: function and evolution* (eds GE Hill, KJ McGraw), pp. 417–454. Cambridge, MA: Harvard University Press.
5. Irwin RE. 1994 The evolution of plumage dichromatism in the New World blackbirds: social selection on female brightness. *Am. Nat.* **144**, 890–907. (doi:10.1086/285717)
6. Martin TE, Badyaev AV. 1996 Sexual dichromatism in birds: importance of nest predation and nest location for females versus males. *Evolution* **50**, 2454–2460. (doi:10.2307/2410712)
7. Hofmann CM, Cronin T, Omland KE. 2006 Using spectral data to reconstruct evolutionary changes in coloration: carotenoid color evolution in New World orioles. *Evolution* **60**, 1680–1691. (doi:10.1111/j.0014-3820.2006.tb00512.x)
8. Friedman NR, Hofmann CM, Kondo B, Omland KE. 2009 Correlated evolution of migration and sexual dichromatism in the New World orioles (*Icterus*). *Evolution* **63**, 3269–3274. (doi:10.1111/j.1558-5646.2009.00792.x)
9. Kraaijeveld K, Kraaijeveld-Smit FJL, Komdeur J. 2007 The evolution of mutual ornamentation. *Anim. Behav.* **74**, 657–677. (doi:10.1016/j.anbehav.2006.12.027)
10. Price JJ, Lanyon SM, Omland KE. 2009 Losses of female song with changes from tropical to temperate breeding in the New World blackbirds. *Proc. R. Soc. B* **276**, 1971–1980. (doi:10.1098/rspb.2008.1626)
11. Murphy TG, Rosenthal MF, Montgomerie R, Tarvin KA. 2009 Female American goldfinches use

- carotenoid-based bill coloration to signal status. *Behav. Ecol.* **20**, 1348–1355. (doi:10.1093/beheco/arp140)
12. Crowhurst CJ, Zanollo V, Griggio M, Robertson J, Kleindorfer S. 2012 White flank spots signal feeding dominance in female diamond firetails, *Stagonopleura guttata*. *Ethology* **118**, 63–75. (doi:10.1111/j.1439-0310.2011.01986.x)
 13. Price T, Birch GL. 1996 Repeated evolution of sexual color dimorphism in passerine birds. *Auk* **113**, 842–848. (doi:10.2307/4088862)
 14. Price JJ, Eaton MD. 2014 Reconstructing the evolution of sexual dichromatism: current color diversity does not reflect past rates of male and female change. *Evolution* **68**, 2026–2037. (doi:10.1111/evo.12417)
 15. Hofmann CM, Cronin TW, Omland KE. 2008 Evolution of sexual dichromatism. 1. Convergent losses of elaborate female coloration in New World orioles (*Icterus* spp.). *Auk* **125**, 778–789. (doi:10.1525/auk.2008.07112)
 16. Burns KJ. 1998 A phylogenetic perspective on the evolution of sexual dichromatism in tanagers (Thraupidae): the role of female versus male plumage. *Evolution* **52**, 1219–1224. (doi:10.2307/2411252)
 17. Wiens JJ. 2001 Widespread loss of sexually selected traits: how the peacock lost its spots. *Trends Ecol. Evol.* **16**, 517–523. (doi:10.1016/S0169-5347(01)02217-0)
 18. Amundsen T. 2000 Why are female birds ornamented? *Trends Ecol. Evol.* **15**, 149–155. (doi:10.1016/S0169-5347(99)01800-5)
 19. Bailey SF. 1978 Latitudinal gradients in colors and patterns of passerine birds. *Condor* **80**, 372–381. (doi:10.2307/1367187)
 20. Badyaev AV, Hill GE. 2003 Avian sexual dichromatism in relation to phylogeny and ecology. *Annu. Rev. Ecol. Syst.* **34**, 27–49. (doi:10.1146/annurev.ecolsys.34.011802.132441)
 21. Scott DK, Clutton-Brock TH. 1990 Mating systems, parasites and plumage dimorphism in waterfowl. *Behav. Ecol. Sociobiol.* **26**, 261–273. (doi:10.1007/BF00178319)
 22. Hamilton TH. 1961 On the functions and causes of sexual dimorphism in breeding plumage characters of North American species of warblers and orioles. *Am. Nat.* **95**, 121–123. (doi:10.1086/282167)
 23. Lindström Å. 1989 Finch flock size and risk of hawk predation at a migratory stopover site. *Auk* **106**, 225–232.
 24. Alerstam T, Hedenström A, Åkesson S. 2003 Long-distance migration: evolution and determinants. *Oikos* **2**, 247–260. (doi:10.1034/j.1600-0706.2003.12559.x)
 25. Caldwell GS. 1986 Predation as a selective force on foraging herons: effects of plumage color and flocking. *Auk* **103**, 494–505.
 26. Slagsvold T, Dale S, Kruszewicz A. 1995 Predation favours cryptic coloration in breeding male pied flycatchers. *Anim. Behav.* **50**, 1109–1121. (doi:10.1016/0003-3472(95)80110-3)
 27. Huhta E, Rytönen S, Solonén T. 2003 Plumage brightness of prey increases predation risk: an among-species comparison. *Ecology* **84**, 1793–1799. (doi:10.1890/0012-9658(2003)084[1793:PBOPIP]2.0.CO;2)
 28. Lok T, Overdijk O, Piersma T. 2015 The cost of migration: spoonbills suffer higher mortality during trans-Saharan spring migrations only. *Biol. Lett.* **11**, 20140944. (doi:10.1098/rsbl.2014.0944)
 29. Stutchbury BJM, Morton ES. 2001 *Behavioral ecology of tropical birds*. San Diego, CA: Academic Press.
 30. Tobias JA, Gamarra-Toledo V, García-Olaechea D, Pulgarín PC, Seddon N. 2011 Year-round resource defence and the evolution of male and female song in suboscine birds: social armaments are mutual ornaments. *J. Evol. Biol.* **24**, 2118–2138. (doi:10.1111/j.1420-9101.2011.02345.x)
 31. Illes AE. 2015 Context of female bias in song repertoire size, singing effort, and singing independence in a cooperatively breeding songbird. *Behav. Ecol. Sociobiol.* **69**, 139–150. (doi:10.1007/s00265-014-1827-3)
 32. West-Eberhard MJ. 1979 Sexual selection, social competition, and evolution. *Proc. Am. Phil. Soc.* **123**, 222–234.
 33. West-Eberhard MJ. 1983 Sexual selection, social competition, and speciation. *Q. Rev. Biol.* **58**, 155–183. (doi:10.1086/413215)
 34. Rubenstein DR, Lovette IJ. 2009 Reproductive skew and selection on female ornamentation in social species. *Nature* **462**, 786–789. (doi:10.1038/nature08614)
 35. Rubenstein DR. 2012 Sexual and social competition: broadening perspectives by defining female roles. *Phil. Trans. R. Soc. B* **367**, 2248–2252. (doi:10.1098/rstb.2011.0278)
 36. Murphy TG, Hernández-Muciño D, Osorio-Beristain M, Montgomerie R, Omland KE. 2009 Carotenoid-based status signaling by females in the tropical streak-backed oriole. *Behav. Ecol.* **20**, 1000–1006. (doi:10.1093/beheco/arp089)
 37. Whittingham LA, Kirkconnell A, Ratcliffe LM. 1992 Differences in song and sexual dimorphism between Cuban and North American red-winged blackbirds (*Agelaius phoeniceus*). *Auk* **109**, 928–933. (doi:10.2307/4088178)
 38. Tobias JA, Montgomerie R, Lyon BE. 2012 The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. *Phil. Trans. R. Soc. B* **367**, 2274–2293. (doi:10.1098/rstb.2011.0280)
 39. Catchpole CK. 1980 Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. *Behaviour* **74**, 149–166. (doi:10.1163/156853980X00366)
 40. Catchpole CK. 1982 The evolution of bird sounds in relation to mating and spacing behavior. In *Acoustic communication in birds*, vol. 1 (eds DE Kroodsma, EH Miller, H Ouellets), pp. 297–319. New York, NY: Academic Press.
 41. Jennions MD, Petrie M. 1997 Variation in mate choice and mating preferences: a review of causes and consequences. *Biol. Rev.* **72**, 283–327. (doi:10.1017/S0006323196005014)
 42. Stutchbury BJ, Morton ES. 1995 The effect of breeding synchrony on extra-pair mating systems in songbirds. *Behaviour* **132**, 675–690. (doi:10.1163/156853995X00081)
 43. Spottiswoode C, Møller AP. 2004 Extrapair paternity, migration, and breeding synchrony in birds. *Behav. Ecol.* **15**, 41–57. (doi:10.1093/beheco/arg100)
 44. Del Hoyo J, Elliott A, Christie DA. 2010 *Handbook of the birds of the world*, vol. 15. *Weavers to New World warblers*. Barcelona, Spain: Lynx Edicions.
 45. Winger BM, Lovette IJ, Winkler DW. 2012 Ancestry and evolution of seasonal migration in the Parulidae. *Proc. R. Soc. B* **279**, 610–618. (doi:10.1098/rspb.2011.1045)
 46. Lovette IJ *et al.* 2010 A comprehensive multilocus phylogeny for the wood-warblers and a revised classification of the Parulidae (Aves). *Mol. Phylogenet. Evol.* **57**, 753–770. (doi:10.1016/j.ympev.2010.07.018)
 47. Martin PR, Montgomerie R, Loughheed SC. 2010 Rapid sympatry explains greater color pattern divergence in high latitude birds. *Evolution* **64**, 336–347. (doi:10.1111/j.1558-5646.2009.00831.x)
 48. Dunn PO, Whittingham LA, Pitcher TE. 2001 Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution* **55**, 161–175. (doi:10.1111/j.0014-3820.2001.tb01281.x)
 49. Montgomerie R. 2006 Analyzing colors. In *Bird coloration volume 1: mechanisms and measurements* (eds GE Hill, KJ McGraw), pp. 70–147. Cambridge, MA: Harvard University Press.
 50. Armenta JK, Dunn PO, Whittingham LA. 2008 Quantifying avian sexual dichromatism: a comparison of methods. *J. Exp. Biol.* **211**, 2423–2430. (doi:10.1242/jeb.013094)
 51. Seddon N, Tobias JA, Eaton M, Ödeen A. 2010 Human vision can provide a valid proxy for avian perception of sexual dichromatism. *Auk* **127**, 283–292. (doi:10.1525/auk.2009.09070)
 52. Hijmans RJ, Guarino L, Bussinc C, Mathur P, Cruz M, Barrettes I, Rojas R. 2004 A geographic information system for the analysis of species distribution data. See www.diva-gis.org.
 53. Ridgely RS, Allnutt TF, Brooks T, McNicol DK, Mehlman DW, Young BE, Zook JR. 2003 *Digital distribution maps of the birds of the western hemisphere*, v. 1. Arlington, TX: NatureServe.
 54. Ersts PJ. Geographic Distance Matrix Generator (v. 1.2.3). American Museum of Natural History, Center for Biodiversity and Conservation. See http://biodiversityinformatics.amnh.org/open_source/gdmg.
 55. R Development Core Team. 2012 R: a language and environment for statistical computing. See <http://www.r-project.org>.
 56. Revell LJ. 2010 Phylogenetic signal and linear regression on species data. *Methods Ecol. Evol.* **1**, 319–329. (doi:10.1111/j.2041-210X.2010.00044.x)
 57. Garland T, Dickerman AW, Janis CM, Jones JA. 1993 Phylogenetic analysis of covariance by computer simulation. *Syst. Biol.* **42**, 265–292. (doi:10.1093/sysbio/42.3.265)

58. Revell LJ. 2012 phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**, 217–223. (doi:10.1111/j.2041-210X.2011.00169.x)
59. Burnham KP, Anderson DR. 2002 *Model selection and multimodel interface: a practical information-theoretic approach*, 2nd edn. New York, NY: Springer.
60. Cohen J, Cohen P, West SG, Aiken LS. 2003 *Applied multiple regression/correlation analysis for the behavioral sciences*, 3rd edn. Mahwah, NJ: Lawrence Erlbaum Associate.
61. Pinheiro J, Bates D, DebRoy S, Sarkar D, Team RDC. 2013 nlme: linear and nonlinear mixed effects models. R package v. 3.1-113. See <http://cran.r-project.org/web/packages/nlme/index.html>.
62. Paradis E, Claude J, Strimmer K. 2004 APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290. (doi:10.1093/bioinformatics/btg412)
63. Maddison WP. 1990 A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution* **44**, 539–557. (doi:10.2307/2409434)
64. Maddison DR, Maddison WP. 2000 MacCLADE: analysis of phylogeny and character evolution, v. 4.0. See <http://macclade.org/macclade.html>.
65. Pagel M. 1994 Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proc. R. Soc. Lond. B* **255**, 37–45. (doi:10.1098/rspb.1994.0006)
66. Maddison WP, Maddison DR. 2009 MESQUITE: a modular system for evolutionary analysis, v. 2.6. See <https://mesquiteproject.wikispaces.com>.
67. Schluter D, Price T, Mooers AØ, Ludwig D. 1997 Likelihood of ancestor states in adaptive radiation. *Evolution* **51**, 1699–1711. (doi:10.2307/2410994)
68. Rohwer S. 1975 The social significance of avian plumage variability. *Evolution* **29**, 593–610. (doi:10.2307/2407071)
69. Karubian J. 2013 Female ornamentation in *Malurus* fairy-wrens: a hidden evolutionary gem for understanding female perspectives on social and sexual selection. *EMU* **113**, 248–258. (doi:10.1071/MU12093)
70. Sillett TS, Holmes RT. 2002 Variation in survivorship of a migratory songbird throughout its annual cycle. *J. Anim. Ecol.* **71**, 296–308. (doi:10.1046/j.1365-2656.2002.00599.x)
71. Yoder JM, Marschall EA, Swanson DA. 2004 The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. *Behav. Ecol.* **15**, 469–476. (doi:10.1093/beheco/arih037)
72. Fitzpatrick S. 1994 Colourful migratory birds: evidence for a mechanism other than parasite resistance for the maintenance of 'good genes' sexual selection. *Proc. R. Soc. Lond. B* **257**, 155–160. (doi:10.1098/rspb.1994.0109)
73. Hill GE. 2000 Energetic constraints on expression of carotenoid-based plumage coloration. *J. Avian Biol.* **31**, 559–566. (doi:10.1034/j.1600-048X.2000.310415.x)
74. McGraw KJ, Hill GE, Parker RS. 2005 The physiological costs of being colourful: nutritional control of carotenoid utilization in the American goldfinch, *Carduelis tristis*. *Anim. Behav.* **69**, 653–660. (doi:10.1016/j.anbehav.2004.05.018)
75. Tarvin KA, Murphy TG. 2012 It isn't always sexy when both are bright and shiny: considering alternatives to sexual selection in elaborate monomorphic species. *Ibis* **154**, 439–443. (doi:10.1111/j.1474-919X.2012.01251.x)